

BROMUS AYACUCHENSIS (POACEAE: POOIDEAE: BROMEAE),
A NEW SPECIES FROM PERU, WITH
A KEY TO BROMUS IN PERU

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ABSTRACT

Bromus ayacuchensis, a new species from Departamento Ayacucho, Peru, is described and illustrated. The new species is similar to species in *Bromus* sect. *Ceratochloa*, particularly *B. cebadilla*, because of its strongly keeled lemmas. It differs from *B. cebadilla* by having densely pilose culms near the base, adaxially pilose ligules 3–6.6 mm long, lower glumes 1-veined, upper glumes 3-veined, pilose lemmas (especially along the margins and near the apex), lemma margins that are tightly involute on lower 1/5–1/4, and lemma awns 3–5.5 mm long. Phylogenetic analyses of sequence data from the internal transcribed spacer regions of nuclear ribosomal DNA place *B. ayacuchensis* in a clade with species of sect. *Ceratochloa*, whereas analyses of plastid data from the *trnL* intron and the 3'-end of *ndhF* indicate that *B. ayacuchensis* is closely related to this clade. Confirmed records are provided for *B. modestus* and *B. cebadilla* in Peru, and *B. coloratus* and *B. flexuosus* are reported for the first time in Peru. A key to the 12 species of *Bromus* now known from Peru is included.

RESUMEN

Se describe y se ilustra **Bromus ayacuchensis** Saarela & P.M. Peterson, sp. nov., una nueva especie del Departamento de Ayacucho, Perú. La nueva especie es similar a las especies de *Bromus* secc. *Ceratochloa*, particularmente *B. cebadilla*, porque tiene lemas muy carenadas. Se diferencia de *B. cebadilla* por tener culmenes densamente pilosos cerca de la base, lígulas 3–6.6 mm de largo y pilosas en la parte ventral superior, glumas inferiores con 1 nervio, glumas superiores con 3 nervios, lemas pilosos (especialmente a lo largo de los márgenes y cerca del ápice), los márgenes del lema son firmemente involutos en la porción 1/5–1/4 inferior del lema y aristas de 3–5.5 mm de largo. Los análisis filogenéticos de los datos de la secuencia de ADN de las regiones transcritas internas del espaciador ribosómico nuclear colocan a *B. ayacuchensis* en un clado con las especies de la sect. *Ceratochloa*, mientras que los análisis de los datos del intrón del plástido del *trnL* y de los extremos 3' del *ndhF* indican que *B. ayacuchensis* está íntimamente relacionado pero no es parte de este clado. Proporcionamos ejemplares de especímenes *B. modestus* y *B. cebadilla* provenientes del Perú, y *B. coloratus* y *B. flexuosus* encontrados por primera vez en Perú. Se incluye la clave para las 12 especies de *Bromus* conocidas en Perú.

Bromus L. (Poaceae: Pooideae: Bromeae) is a large genus of grasses with over 160 species distributed throughout temperate regions of the world (Clayton & Renvoize 1986). Some species are important forage grasses (e.g., *B. inermis* Leyss.; *B. auleticus* Trin. ex Nees), and many are highly aggressive, invasive weeds (e.g., *B. diandrus* Roth; *B. madritensis* L.; *B. tectorum* L.; Pavlick 1995).

Bromus is distinguished from other grass genera by the combination of leaf sheath

margins that are connate (closed) for most of their length, awns that are inserted subapically on the lemmas (except in *B. lepidus* Holm. and *B. bidentatus* Holmström & H. Scholz; Holmstrom & Scholz 2000), hairy apical bilabiate-appendages of the ovary, and simple starch grains (Wagnon 1952; Smith 1970; Clayton & Renvoize 1986).

Bromus is diverse morphologically and has been divided variously into segregate genera [*Anisantha* C. Koch, *Boissiera* Hochst. ex Steud., *Bromus*, *Bromopsis* (Dumort.) Fourr., *Ceratochloa* P. Beauv., *Nevskiella* Kreczetowicz & Vvedensky, and *Trisetobromus* Nevski], subgenera [*Bromus*, *Stenobromus* (Hack.), *Festucaria* Gren. & Godr., *Ceratochloa* (P. Beauv.) Hack., *Nevskiella* (Kreczetowicz & Vvedensky) Kreczetowicz & Vvedensky, and *Neobromus* Shear; Stebbins 1981] or sections [*Bromus*, *Triniusia* (Steud.) Nevski., *Boissiera* (Hochst. ex Steud.) P. M. Sm., *Genea* Dumort., *Bromopsis* Dumort., *Ceratochloa* (P. Beauv.) Griseb., *Nevskiella* (Kreczetowicz & Vvedensky) Tournay, and *Neobromus* (Shear) Hitchc.; Smith 1970]. Most recent workers use a sectional classification (e.g., Clayton & Renvoize 1986; Pavlick 1995; Planchuelo & Peterson 2000; Pavlick et al. 2003).

Molecular studies (Pillay & Hilu 1990, 1995; Ainouche & Bayer 1997; Saarela et al. in press) support the monophyly of some of these sections (e.g., *Bromus* sects. *Bromus*, *Genea*, *Ceratochloa*), and have indicated that others comprise several distinct lineages (e.g., *Bromus* sect. *Bromopsis*). Incongruence between plastid and nuclear ribosomal gene trees has provided tentative insight into past hybridization events in the genus (Saarela et al. in press). The available classification schemes (e.g., Smith 1970) do not satisfactorily reflect evolutionary relationships in the genus as understood currently (Saarela et al. in press).

Approximately 80 native and introduced species of *Bromus* are recognized currently in North, South, and Central America (Pavlick et al. 2003). Many regional treatments of *Bromus* have been published (Wagnon 1952; Soderstrom & Beaman 1968; Cámara Hernández 1978; Pinto-Escobar 1981, 1986; Matthei 1986; Pavlick 1995; Gutiérrez & Pensiero 1998; Planchuelo & Peterson 2000; Pavlick et al. 2003), cytological, genetical, and anatomical studies are revealing new information (e.g., Martinello & Schifino-Wittman 2003; Ramos et al. 2002; Fu et al. 2005; Tuna et al. 2005, 2006), taxonomic studies are clarifying species circumscriptions (e.g., Naranjo et al. 1990; Planchuelo 1991; Naranjo 1992; Peterson et al. 2002; Oja et al. 2003; Massa et al. 2001, 2004; Saarela et al. 2005) and new taxa are being described (e.g., Matthei 1986; Renvoize 1994; Peterson & Planchuelo 1998).

On a recent trip to Peru, the second and third authors collected several unusual individuals of *Bromus* with strongly keeled (laterally flattened) lemmas, 1-veined lower glumes, and 3-veined upper glumes. Strongly keeled lemmas are characteristic of sect. *Ceratochloa*, but all known species from this section have 3–9-veined lower glumes and 5–9-veined upper glumes (Smith 1970). Known species of *Bromus* that have 1- and 3-veined lower and upper glumes, respectively, have lemmas that are wide and short, rounded, or slightly keeled (Smith 1970). A review of the taxonomic literature and specimens in the US National Herbarium has indicated that no individuals of *Bromus* with this combination of characters have been described previously. We name and describe these recent collections as a new species, *Bromus ayacuchensis*. We discuss the phylogenetic placement of the new species in the genus based on its morphology and DNA sequence data from the internal transcribed spacer (ITS) regions of nuclear ribosomal DNA, the plastid *trnL*(UAA) intron, and the 3'-end of the plastid *ndhF* gene.

MATERIALS AND METHODS

The morphological description of the new species is based on material from three collec-

tions (see below). Fifteen specimens were measured for the morphological description. To characterize leaf anatomy, leaf blades were field collected, and segments of about 5 mm in length from the middle of the second leaf blade below the inflorescence of the flowering culm were fixed in FPA (formalin: propionic acid: ethyl alcohol: water; 2:1:10:7). Leaf blades were desilicified in 30%-hydrofluoric acid for 48 hours. Leaf blade segments were dehydrated, embedded, sectioned, and stained following the methods described in Columbus (1999). Terminology used in the anatomical description follows Metcalfe (1960) and Acedo & Llamas (1999).

DNA was obtained from field collected leaf material of two collections (Peterson 16452 & Refilio-Rodríguez and Peterson 18212 & Refilio-Rodríguez). Voucher specimens are deposited in US. Sequence data were obtained for *B. ayacuchensis* from the plastid *trnL*(UAA) intron, the 3'-end of the plastid *ndhF* gene, and the internal transcribed spacer (ITS) regions of nuclear ribosomal DNA, following the protocol in Saarela et al. (in press). Sequences for all regions from both individuals were identical, thus a single consensus sequence was generated for each region. Sequence data have been deposited in GenBank with the following accessions: (ITS: DQ676867; 3' *ndhF*: DQ676868; *trnL* intron: DQ676866). The new sequence data were added to an existing matrix that includes sequence data from 46 species of *Bromus* that represent a large proportion of the morphological and geographical diversity in the genus (Saarela et al. in press). Heuristic searches using parsimony were conducted independently on the nuclear ribosomal DNA and combined plastid data sets with 100 random starting trees, tree-bisection-reconnection (TBR) branch swapping, and all character and character-state changes equally weighted. Branch support was assessed using maximum parsimony bootstrap analysis (Felsenstein 1985) from 500 replicates using the heuristic search option, with one random starting tree, TBR branch swapping, and Max Trees set to 500 per replicate.

RESULTS AND DISCUSSION

Morphological and molecular data suggest that *B. ayacuchensis* is similar to species classified in *Bromus* sect. *Ceratochloa*. *Bromus ayacuchensis* shares the strongly laterally compressed spikelets with species in sect. *Ceratochloa*, and the nuclear ribosomal trees include it in a clade with species of *Bromus* sect. *Ceratochloa* (BS=92%; Fig. 1a). *Bromus* sect. *Ceratochloa* is native to North and South America, characterized by a perennial habit, ovate-lanceolate strongly laterally compressed spikelets, 3-5-veined lower glumes, 5-7-veined upper glumes, and strongly keeled lemmas (Smith 1970). All taxa in the section are polyploids (octo-, hexa-, and 12-ploid) (Stebbins 1981; Pavlick 1995). In the first complete synopsis of *Bromus* in South America, Planchuelo & Peterson (2000) recognized nine species in sect. *Ceratochloa*. A recent taxonomic study has proposed the lumping of several hexaploid taxa from Patagonia [*B. catharticus* Vahl, *B. cebadilla* Steud. (syn. = *B. stamineus* E. Desv.), *B. coloratus* Steud., *B. lithobius* Trin., *B. mango* E. Desv., and *B. tunicatus* Phil] into one morphologically variable species, *B. catharticus* (Massa et al. 2001, 2004). Other species of sect. *Ceratochloa* recognized currently in South America include *B. bonariensis* Parodi & J.A. Cámara, an endemic of Provincia Buenos Aires, Argentina, and *B. striatus* Hitchc., an endemic of Peru (Planchuelo & Peterson 2000; Pavlick et al. 2003). These species were outside of the geographic scope of the studies by Massa et al. (2001, 2004), but both have been considered conspecific with *B. catharticus* in the past (Pinto-Escobar 1986; Planchuelo 1991). Among these taxa, *B. ayacuchensis* is most similar to *B. cebadilla*, a species known from Argentina, Chile, Peru, and the USA (Pavlick et al. 2003).

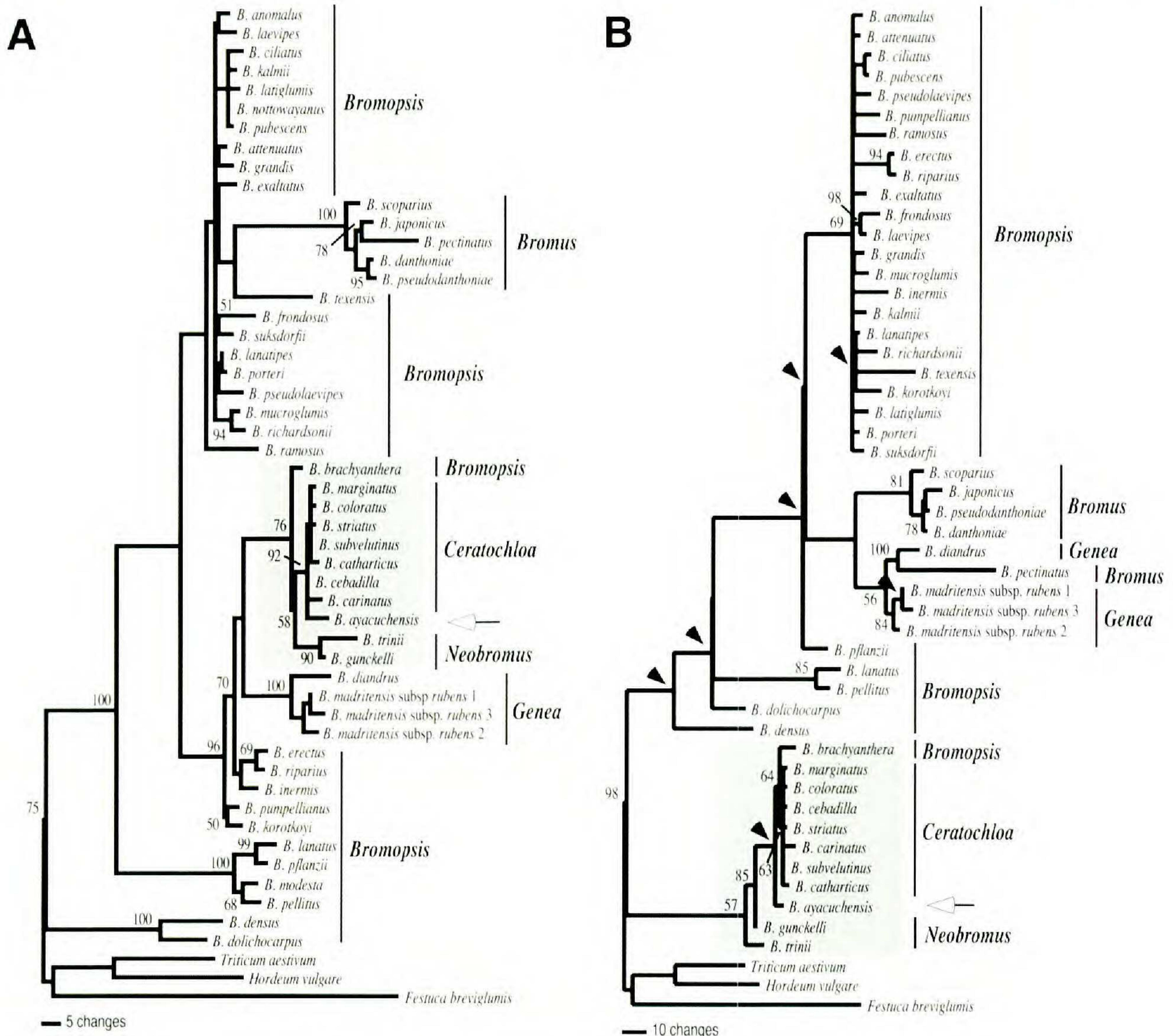


FIG. 1. Phylogenetic position of *Bromus ayacuchensis* based on sequence data from: (A) the internal transcribed spacer (ITS) regions of nuclear ribosomal DNA. The position of *B. ayacuchensis* in each tree is indicated with an open arrow. Bootstrap support values are indicated above or below the branches. Clades that collapse in the strict consensus tree are indicated with diagonal arrows. Traditionally recognized sections in *Bromus* (sensu Smith 1970) are indicated to the right of the trees; and (B) the combined plastid *trnL* intron and 3'-end of *ndhF*.

Bromus ayacuchensis differs from *B. cebadilla* by having densely pilose culms near the base, adaxially pilose ligules 3–6.6 mm long, lower glumes 1-veined, upper glumes 3-veined, pilose lemmas (especially along the margins and near the apex), lemma margins that are tightly involute on lower 1/5–1/4, and lemma awns 3–5.5 mm long. The leaf blade of *B. ayacuchensis* (Fig. 4) is anatomically similar to the leaf blade of *B. catharticus* (the only taxon in sect. *Ceratochloa* for which anatomical data exist; Acedo & Llamas 1999). It has a well-developed keel, well-differentiated bulliform cells, and lower-order vascular bundles associated with sclerenchyma.

Morphological and molecular data also identify some differences between *B. ayacuchensis* and species classified in sect. *Ceratochloa*. *Bromus ayacuchensis* differs from taxa classified in sect. *Ceratochloa* by its 1- and 3- veined lower glumes. In the plastid trees, *B. ayacuchensis* is weakly supported as the sister group of a clade that comprises *Bromus* sect. *Ceratochloa* and *B. brachyanthera*, and these taxa are part of a larger clade that also includes species of sect. *Neobromus* (Fig. 1b). Among South American *Bromus*

species, 1- and 3-veined lower and upper glumes are found in taxa traditionally classified within *Bromus* sections *Bromopsis*, *Genea*, and *Neobromus* (Smith 1970). The two species classified in the closely-related sect. *Neobromus* are distinguished from *B. ayacuchensis* by their narrowly elliptic spikelets, lemmas with a deep apical sinus, and geniculate awns (Smith 1970; Matthei 1986). Species of sect. *Genea* in South America, which are all introduced, are easily separated from *B. ayacuchensis* by their oblong or wedge-shaped spikelets and narrow and elongate lemmas with long awns (Smith 1970). *Bromus* sect. *Bromopsis* is likely a paraphyletic assemblage of species (Saarela et al. in press) that have 1(-3)- and 3(-5)-veined lower and upper glumes, similar to *B. ayacuchensis*. The strongly laterally compressed spikelets and lemmas of *B. ayacuchensis* separate it from this artificial group of species, which have spikelets and lemmas that are terete and dorsally flattened or sometimes slightly keeled (Smith 1970), although the plastid and nuclear molecular data indicate that one species of sect. *Bromopsis* from South America, *B. brachyanthera*, is closely related to *B. ayacuchensis* and sect. *Ceratochloa* (Figs. 1a, b). The molecular data and mixed morphological characters suggest that *B. ayacuchensis* might have originated via hybridization between a species of sect. *Ceratochloa* and a species of the non-monophyletic sect. *Bromopsis*. Sampling of additional South American species of sect. *Bromopsis* will be necessary to determine if any are part of the clade that includes sects. *Neobromus*, *Ceratochloa*, *B. brachyanthera* and *B. ayacuchensis*.

Nine species of *Bromus* (*B. berteroanus* Colla; *B. catharticus*; *B. cebadilla*; *B. lanatus* Kunth; *B. modestus* Renvoize; *B. pitensis* Kunth; *B. segetum* Kunth; *B. striatus* Hitchc.; *B. villosissimus* Hitchc.) are currently known and verified by us from Peru (Planchuelo & Peterson 2000; Tovar 1993). *Bromus carinatus* Hook. & Arn. and *B. inermis* Leyss. have also been listed for Peru but these records are doubtful (Brako & Zarucchi 1994). *Bromus cebadilla* has been reported from the country previously without citation of specimens (Renvoize 1998; Pavlick et al. 2003). We provide confirmed records of this taxon in Appendix 1. *Bromus modestus* is a recently described species (Renvoize 1994), and we report additional collections from Peru in Appendix 1. We have also collected *B. coloratus* and *B. flexuosus* Planchuelo in Peru (Planchuelo 1983), and report these collections here for the first time (Appendix 1). With the discovery of *B. ayacuchensis*, and confirmed records of *B. coloratus* and *B. flexuosus*, the number of *Bromus* species known from Peru is 12. A new key to *Bromus* in Peru is provided below.

TAXONOMIC TREATMENT

Bromus ayacuchensis Saarela & P.M. Peterson, sp. nov. (Fig. 2).

TYPE: PERU. DEPARTAMENTO AYACUCHO: Provincia Lucanas, 12 km E of Puquio on road towards Cuzco, (14°41'19.2"S Lat, 74°04'28.3"W Long), 3730 m, among large boulders with *Berberis* (Berberidaceae), above meadow with small creek, 11 Mar 2002, P.M. Peterson 16452 & N.F. Refulio-Rodríguez (HOLOTYPE: US; ISOTYPES: K!, MO!, UBC!, USM!).

A *Bromo cebadilla* Steud. culmis pilosis basilaribus, adaxialibus pilosis 3-6.6 mm longis ligulis, inferioribus 1-nervatis glumis, superioribus 3-nervatis glumis, pilosis lemmatibus (praecipue apud margines et apicem), lemmatum marginibus inferioribus 1/5-1/4 involventibus, lemmatum aristis 3-5.5 mm longis, recedit.

Loosely caespitose perennials, rhizomes short with extravaginal shoot initiation. Culms (30-)50-120 cm tall, erect to slightly decumbent near base, pilose, densely pilose near base; internodes somewhat glabrous to sparsely pilose, retrorsely pilose just above dark brownish nodes. Sheaths 8-20 cm long, mostly longer than internodes below and shorter than internodes above, closed on lower 2/3-3/4, retrorsely pilose, hairs 0.7-1.6 mm long; margins smooth; cataphylls and lower sheaths densely pilose, often shredding. Ligules



FIG. 2. *Bromus ayacuchensis* (Peterson 16452 & Refulio-Rodríguez). A. Habit. B. Inflorescence. C. Sheath, ligule, and base of blade. D. Spikelet. E. Lower glume, dorsal view. F. Upper glume, dorsal view. G. Lemma, dorsal view. H. Floret, ventral view. I. Floret, lateral view. J. Base of floret with rachilla segment. K. Palea with lodicules and stamens, ventral view. L. Palea with rachilla segment and stamens, dorsal view. M. Lodicules, stamens, and pistil. N. Lodicules. O. Gynoecium, mature. P. Caryopsis.

3–6.6 mm long, membranous, pilose adaxially; apex obtuse, erose. Blades 20–55 cm long, 3–8 mm wide, flat, apically acuminate, mostly sparingly pilose below and glabrous to sparingly pilose above with hairs 0.5–1.2 mm long; margins scabrous. Panicles 12–25 cm long, 1–8 cm wide, obovate, lax, often nodding; central axis glabrous or with an occasional hair; branches mostly 1.5–10 cm long, ascending or appressed to spreading and drooping, naked near base, often re-branched immediately at base, scabrous, hairs antrorse and stiff; lower inflorescence nodes usually with 2–4 branches. Spikelets (12–)18–27 mm long, florets 5–8, laterally compressed; lowest rachilla internodes 2–3 mm long. Glumes 5–11.2 mm long, glabrous or sparsely hairy; apex entire or mucronate, the mucro usually ≤ 1 mm long; lower glumes 5–8 mm long, 1-veined, apex acuminate; upper glumes 8–11.2 mm long, 3-veined, apex acute. Lemmas 10–12.6 mm long, chartaceous, 5- or 7-veined, pilose, especially along margins and near apex, hairs 0.2–0.5 mm long; margins tightly involute on lower 1/5–1/4; apex entire or minutely bifid, teeth ≤ 0.2 mm long, awned, awn 3–5.5 mm long, straight. Paleas 9–12 mm long, shorter than lemma, membranous to hyaline, ciliate along keel, glabrous between veins; apex acuminate, sometimes mucronate, veins extending as mucro usually ≤ 1 mm long. Lodicules 1–1.3 mm long, narrowly elliptic to narrowly obovate, unlobed. Stamens 3; anthers 3.1–3.8 mm long, yellowish-orange. Ovaries 1.2–2 mm long, golden brown, hairy on upper 1/2–2/3 with hairs 0.3–0.6 mm long; styles 2, separate; stigmas 2, feathery, whitish. Caryopses 5.8–7 mm long, yellowish-brown, apex hairy, hairs 0.4–0.8 mm long; hilum extending length of grain.

Distribution and Habitat.—Known only from near the type locality 12–15 km E of Puquio on road towards Cuzco between 3730–3790 m on slopes under large boulders and beneath thorny shrubs, such as *Colletia spinosissima* J.F. Gmel. (Rhamnaceae), *Berberis* (Berberidaceae), and *Ribes* (Grossulariaceae); also associated with *Lepidophyllum* (Asteraceae) and *Festuca* (Poaceae). Suitable habitat for *B. ayacuchensis* is estimated to be 5 km² at the type locality (Fig. 3).

Etymology.—The epithet ‘ayacuchensis’ is designated to reflect the known distribution of the new species in Departamento Ayacucho, Peru.

Additional Specimens Examined: **PERU: Departamento Ayacucho:** Provincia Lucanas, 13 km E of Puquio at km 172 marker (14°41'18.5" S Lat, 74°04'26.8" W Long), 8 Apr 2004, P.M. Peterson & N.F. Refulio-Rodríguez 18212 (K, MO, UBC, US, USM); 15 km E of Puquio at Km 174 Marker (14° 41' 42.9"S Lat, 74°03'46.8" W Long), 9 Apr 2004, P.M. Peterson & N.F. Refulio-Rodríguez 18233 (K, MO, UBC, US, USM).

Leaf Anatomy.—The blades (Fig. 4) are flat and have a C₃ anatomy, with completely sclerefied margins. The epidermis is comprised of oval to round, subequal cells. Bulliform cells are 2–4 times the size of the regular epidermal cells, located adaxially, and arranged in groups of 5–6. Stomates are located adaxially and abaxially, and are usually associated with deep sunken pits. The chlorenchyma tissue is of the festucoid type. Vascular bundles are all primary, round in outline, and they are all approximately the same size, with the exception of the larger central rib. Vascular bundles are well differentiated into xylem adaxially and phloem abaxially. Vascular sheaths are double; the inner sheath is sclerenchymatous and complete, whereas the outer sheath is parenchymatous and incomplete. Sclerenchyma fibers are associated adaxially with all bundles, and abaxially with all bundles except those towards the margins of the blade; intercostal sclerenchyma absent. The central structure of the blade is well differentiated, and includes a vascular bundle and a prominent keel comprised of sclerenchyma.



FIG. 3. Geographical distribution of *Bromus ayacuchensis*.

KEY TO THE SPECIES OF BROMUS IN PERU

1. Lemma awns geniculate and twisted; plants short-lived annuals (sect. ***Neobromus***) _____ ***B. berteroanus***
1. Lemma awns straight and not twisted; plants short-lived to long-lived annuals, biennials, or perennials.
 2. Spikelets generally laterally compressed; lemmas laterally compressed and keeled (sect. *Ceratochloa*).
 3. Mature anthers 3–5.5 mm long.
 4. Lower glumes 1-veined; upper glumes 3-veined; culms densely pilose below; ligules adaxially pilose, 3–6.6 mm long; lemmas pilose, especially along the margins and near the apex _____ ***B. ayacuchensis***
 4. Lower glumes 5-veined; upper glumes 7–9-veined; culms glabrous or pubescent below; ligules adaxially glabrous, 2–3 mm long; lemmas glabrous or scabrous throughout _____ ***B. cebadilla***
 3. Mature anthers 0.5–2 mm long.
 5. Lemma awns 12–18(–25) cm long; plants short-lived annuals found only along the coastal desert of Arequipa; panicle branches nodding, drooping and flexuous _____ ***B. striatus***
 5. Lemma awns 0.5–6 mm long; plants long-lived annuals, biennials, or perennials, plants

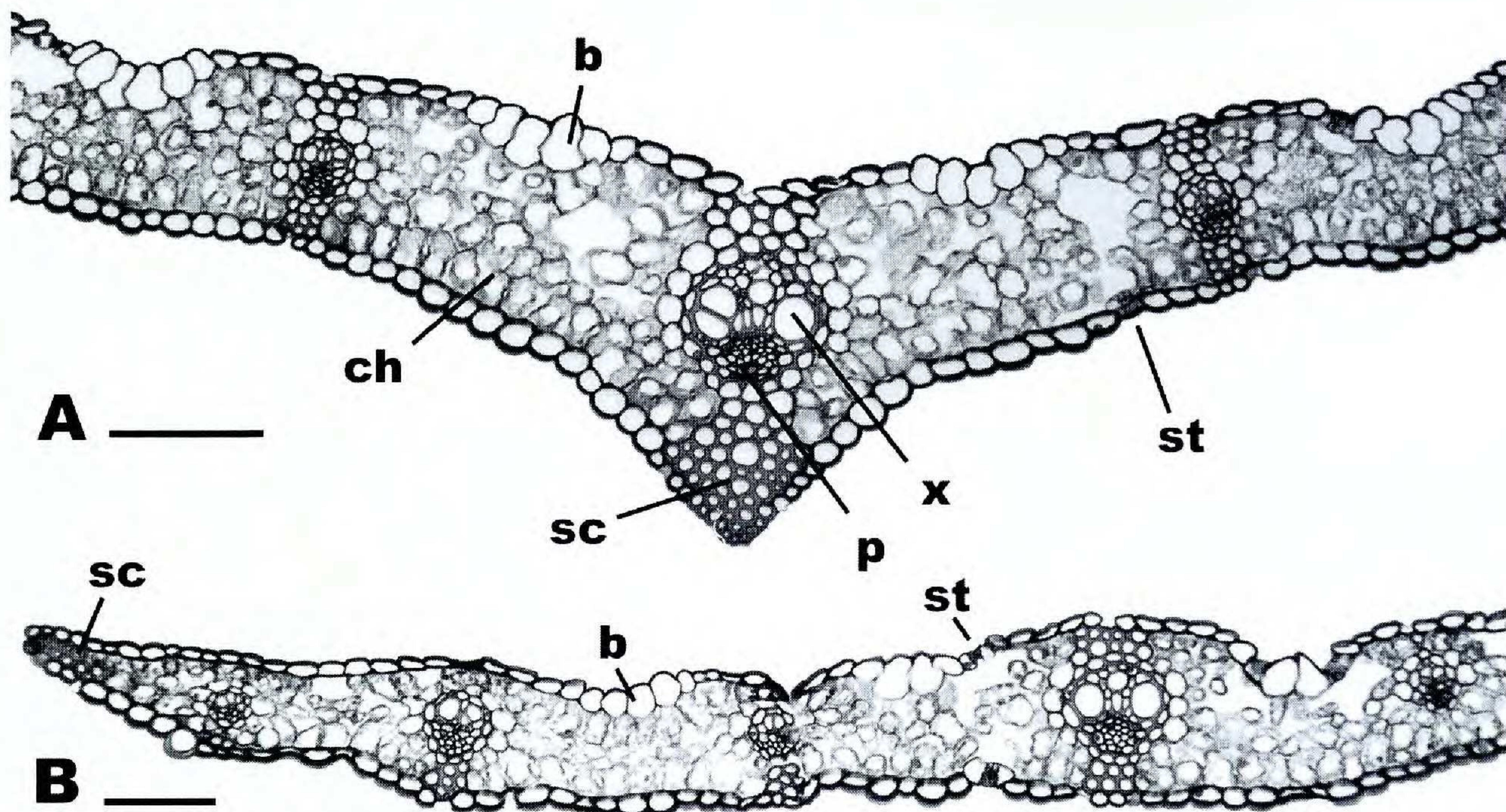


FIG. 4. Leaf anatomy of *Bromus ayacuchensis* [Peterson 18212 & Refilio-Rodríguez (US)]. Transverse section of: A. center of leaf blade (scale bar = 150 μm); B. margin of leaf blade (scale bar = 75 μm). Symbols as follows: b = bulliform cells; ch = chlorenchyma tissue; p = phloem tissue; sc = sclerenchyma tissue; st = stomata; x = xylem tissue.

more wide-ranging; panicle branches usually stiffly erect and ascending, rarely nodding, drooping, or flexuous.

- 6. Lower glumes 5–7(–9)-veined; upper glumes generally 7–9-veined; spikelets strongly laterally compressed _____ ***B. catharticus***
- 6. Lower glumes 3-veined; upper glumes 5-veined; spikelets not strongly laterally compressed _____ ***B. coloratus***
- 2. Spikelets terete or dorsally flattened; lemmas terete or dorsally flattened (sect. ***Bromopsis***).
 7. Culms 5–30(–40) cm tall; leaf blades generally 1–2.5 mm wide.
 8. Spikelets densely villose; panicles 1–3.5 cm long, contracted with short, stiff branches; lemmas hairy _____ ***B. villosissimus***
 8. Spikelets glabrous, scabrous or pilose; panicles 3–8 cm long, open with long, flexuous branches; lemmas glabrous _____ ***B. modestus***
- 7. Culms (15–)30–120 cm tall; leaf blades generally 2–12 mm wide.
 9. Lemma awns (4–)5–9 mm long; lower glumes 0.8–1 mm wide near base.
 10. Pedicels flexuous, erect and reflexed; glumes hairy; pedicels hairy _____ ***B. flexuosus***
 10. Pedicels straight and erect spreading; glumes glabrous; pedicels glabrous _____ ***B. segetum***
- 9. Lemma awns 1–5(–6) mm long; lower glumes 1–3 mm wide near base.
 11. Lower glumes 1–1.2 mm wide near base; pedicels hairy; lemmas villous _____ ***B. lanatus***
 11. Lower glumes 2.2–3 mm wide near base; pedicels glabrous to short pubescent; lemmas glabrous to pubescent, sometimes villous along the margins _____ ***B. pitensis***

APPENDIX 1

Citation of new records and confirmed reports of *Bromus* in Peru.

Bromus cebadilla Steud.—**Cajamarca:** San Miguel: 61 km N of Cajamarca on highway 3N towards Bambamarca, 3640 m, 16 Mar 2000, P.M. Peterson 14914 & N.F. Refilio-Rodríguez (ACOR, US, USM).

Bromus coloratus Steud.—**Arequipa. Caravelí:** 5 km S of Airoca and 3 km N of Cahuacho, 15°28'10.3"S, 73°29'26.6"W, 3520 m, 3 Mar 2002, P.M. Peterson 16390 & M.I. LaTorre, A. Ramírez & D. Susanibar (ACOR, US, USM).

Apurimac. Aymaraes: 9 km SW of Cotaruse on road towards Puquio, 3510 m, 14°29'30.8"S, 73°15'04.2"W, 13 Mar 2002, P.M. Peterson 16480 & N.F. Refilio-Rodríguez (ACOR, US, USM). **Ayacucho. Lucanas:** 6 km E of Puquio on

road towards Chaviña, 14°41'43.9"S, 74°05'35.4"W, 3274 m, 27 Feb 2002, P.M. Peterson 16296 & M.I. LaTorre, A. Ramírez & D. Susanibar (ACOR, US, USM). **Junín. Junín:** 2 km SW of San Jose on road towards Junín, 3970 m, 8 Apr 1997, P.M. Peterson 14121 & N.F. Refulio-Rodríguez (ACOR, USM).

Bromus flexuous Planchuelo.—**Cuzco. Calca:** 22 km N of Calca on road towards Lares, 4120 m, 13°12'56.6"S, 71°54'35.2"W, 16 Mar 2002, P.M. Peterson 16556 & N.F. Refulio-Rodríguez (ACOR, US, USM).

Bromus modestus Renvoize.—**Arequipa:** Sumbay, 4000 m, A. Weberbauer 6902 (F, US). **Huancavelica.** **Huancavelica:** Tansiri near Manta, 4400–4500 m, 4 Apr 1953, O. Tovar 1181 (US, USM). **Ayacucho. Lucanas:** 25 km SE of Puquio on road towards Chaviña, 14°45'17.0"S, 74°03'02.6"W, 3850 m, 27 Feb 2002, P.M. Peterson 16302 & M.I. LaTorre, A. Ramírez & D. Susanibar (US). **Cuzco. Calca:** 30 km N of Claca just below Abra de Amparaes, 13°10'40.2"S, 71°54'09.2"W, 4530 m, 15 Mar 2002, P.M. Peterson 16562 & N.F. Refulio-Rodríguez (ACOR, US, USM). **Puno. Chucuito:** 20 Km E of Huacullani on road towards Desaguadero, 3880 m, 5 Mar 1999, P.M. Peterson 14636 & N.F. Refulio-Rodríguez, F. Salvador-Perez (ACOR, US, USM).

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REFERENCES

- ACEDO, C. and F. LLAMAS. 1999. The genus *Bromus* L. (Poaceae) in the Iberian Peninsula. Phan. Monogr. XXII:1–293.
- AINOUCHE, M.L. and R.J. BAYER. 1997. On the origins of the tetraploid *Bromus* species (section *Bromus*, Poaceae): insights from the internal transcribed spacer sequences of nuclear ribosomal DNA. Genome 40:730–743.
- BRAKO, L., and J.L. ZARUCCHI. 1993. Catalogue of the flowering plants and gymnosperms of Peru. Monogr. Syst. Bot. Missouri Bot. Gard. 45:1–1286.
- CAMARA HERNÁNDEZ, J. 1978. *Bromus* L. In Correa, M.N., ed. Flora Patagónica. Vol. 8. Colecc. Ci. Inst. Nac. Tecnol. Agropecu. III. Buenos Aires, Argentina. Pp. 77–93.
- CLAYTON, W.D. and S.A. RENVOIZE. 1986. Genera Graminum. Grasses of the World. Kew Bull. Add. Ser. 13: 1–389.
- COLUMBUS, J.T. 1999. Morphology and leaf blade anatomy suggest a close relationship between *Bouteloua aristidoides* and *B. (Chondrosium) eriopoda* (Gramineae: Chloridoideae). Syst. Bot. 23: 467–478.
- FELSENSTEIN, J. 1985. Confidence limits on phylogenies: an approach using the bootstrap. Evolution 39:783–791.
- FU, Y.-B., B.E. COULMAN, Y.S.N. FERDINANDEZ, J. CAYOUETTE, and P.M. PETERSON. 2005. Genetic diversity of fringed brome (*Bromus ciliatus*) as determined by amplified fragment length polymorphism. Canad. J. Bot. 83:1322–1328.

- GUTIÉRREZ, H.F. and J.F. PENSIERO. 1998. Sinopsis de las especies Argentinas del género *Bromus* (Poaceae). *Darwiniana* 35:75–114.
- HOLMSTRÖM, G. and H. SCHOLZ. 2000. *Bromus bidentatus* spec. nova and *B. lepidus*, two odd brome-grasses (Gramineae). *Bot. Jahrb. Syst.* 122:195–200.
- MARTINELLO, G.E. and T.T. SCHIFINO-WITTMAN. 2003. Chromosomes of *Bromus aleuticus* Trin. ex Nees (Poaceae). *Genet. Mol. Bio.* 26:369–371.
- MASSA, A.N., S.R. LARSON, K.B. JENSEN, and D.J. HOLE. 2001. AFLP variation in *Bromus* section *Ceratochloa* germplasm of Patagonia. *Crop Sci.* 41:1609–1616.
- MASSA, A.N., K.B. JENSEN, S.R. LARSON, and D.J. HOLE. 2004. Morphological variation in *Bromus* sect. *Ceratochloa* germplasm of Patagonia. *Canad. J. Bot.* 82:136–144.
- MATTHEI, O. 1986. The genus *Bromus* L. (Poaceae) in Chile. *Gayana Bot.* 43:47–110.
- METCALFE, C.R. 1960. *Bromus*. In: Anatomy of Monocotyledons: Gramineae 1. Clarendon Press, Oxford.
- NARANJO, C.A., F.H. ARIAS, F.E. GIL, and A. SORIANO. 1990. *Bromus pictus* of the *B. setifolius* complex (section *Pnigma*): numerical taxonomy and chromosome evidence for species rank. *Canad. J. Bot.* 68: 2493–2500.
- NARANJO, C.A. 1992. Estudios biosistemáticos en especies de *Bromus* (sección *Ceratochloa*, Poaceae). I. Sistemas reproductivos y barreras de aislamiento. *Darwiniana* 31:173–183.
- OJA, T., V. JAASKA, and V. VISLAP. 2003. Breeding system, evolution and taxonomy of *Bromus arvensis*, *B. japonicus* and *B. squarrosus* (Poaceae). *Pl. Syst. Evol.* 242:101–117.
- PAVLICK, L.E. 1995. *Bromus* L. of North America. Royal British Columbia Museum, Victoria.
- PAVLICK, L.E., A.M. PLANCHUELO, P.M. PETERSON, and R.J. SORENG. 2003. *Bromus*. Pp. 154–191. In: Soreng, R.J., P.M. Peterson, G. Davidse, E.J. Judziewicz, F.O. Zuloaga, T.S. Filgueiras, and O. Morrone, Catalogue of New World Grasses (Poaceae): IV. Subfamily Pooideae. *Contr. U.S. Natl. Herb.* 48:1–730.
- PETERSON, P.M. and A.M. PLANCHUELO. 1998. *Bromus catharticus* in South America (Poaceae: Bromeae). *Novon* 8: 53–60.
- PETERSON, P.M., J. CAYOUETTE, Y.S.N. FERNANDEZ, B. COULMAN, and R.E. CHAPMAN. 2002. Recognition of *Bromus richardsonii* and *B. ciliatus*: evidence from morphology, cytology, and DNA fingerprinting (Poaceae: Bromeae). *Aliso* 20:21–36.
- PILLAY, M. and K.W. HILU. 1990. Chloroplast DNA variation in diploid and polyploid species of *Bromus* (Poaceae) subgenera *Festucaria* and *Ceratochloa*. *Theor. Appl. Genet.* 80:326–332.
- PILLAY, M. and K.W. HILU. 1995. Chloroplast-DNA restriction site analysis in the genus *Bromus* (Poaceae). *Amer. J. Bot.* 82: 239–249.
- PINTO-ESCOBAR, P. 1981. The genus *Bromus* in northern South America. *Bot. Jahrb. Syst.* 102:445–457.
- PINTO-ESCOBAR, P. 1986. El genero *Bromus* en Los Andes Centrales de Suramerica. *Caldasia* 15:15–34.
- PLANCHUELO, A.M. 1983. Una nueva especie de *Bromus* (Poaceae) de Argentina. *Kurtziana* 16:123–131.
- PLANCHUELO, A.M. 1991. Estudios sobre el complejo *Bromus catharticus* (Poaceae) I. Evaluación estadística de los caracteres taxonómicos. *Kurtziana* 21:243–257.
- PLANCHUELO, A.M. and P.M. PETERSON. 2000. The species of *Bromus* (Poaceae: Bromeae) in South America. In: Jacobs, S.W.L. and J. Everett, eds. *Grasses: systematics and evolution*. CSIRO, Melbourne. Pp. 89–101.
- RAMOS, J.C., J.C. TIVANO, and A.C. VEGETTI, A.C. 2002. Anatomical studies of reproductive stems of *Bromus aleuticus* Trin. ex Nees. (Poaceae). *Gayana Bot.* 59:51–60.
- RENOVIZE, S.A. 1994. Notes on *Sporobolus* and *Bromus* (Gramineae) from the Andes. *Kew Bull.* 49: 543–546.
- RENOVIZE, S.A. 1998. *Gramineas de Bolivia*. Royal Botanic Gardens, Kew.
- SAARELA, J.M., P.M. PETERSON, R.M. KEANE, J. CAYOUETTE, and S.W. GRAHAM. In Press. Molecular systematics of

- Bromus* (Poaceae:Pooideae) based on chloroplast and nuclear DNA sequence data. In: Columbus, J.T., E.A. Friar, J.M. Porter, L.M. Prince, and M.G. Simpson, eds. Monocots: comparative biology and evolution, 2 vols. Rancho Santa Ana Botanic Garden, Claremont, California, USA.
- SAARELA, J.M., P.M. PETERSON, and J. CAYOUEtte. 2005. *Bromus hallii* (Poaceae), a new combination for California, and taxonomic notes on *B. grandis* and *B. orcuttianus*. *Sida* 21:1997–2013.
- SMITH, P. 1970. Taxonomy and nomenclature of the brome-grasses (*Bromus* L.s.l.). *Notes Roy. Bot. Gard. Edinburgh* 30:361–375.
- SODERSTROM, T.R. and J.H. BEAMAN. 1968. The genus *Bromus* (Gramineae) in Mexico and Central America. *Publ. Mus. Michigan State Univ. Biol. Ser.* 3:465–520.
- STEBBINS, G.L. 1981. Chromosomes and evolution in the genus *Bromus* (Gramineae). *Bot. Jahrb. Syst.* 102:359–379.
- TOVAR, O. 1993. Las Graminees (Poaceae) del Peru. *Ruizia* 13:1–480.
- TUNA, M., K.P. VOGEL, and K. ARUMUGANATHAN. 2005. Genome size and Giemsa C-banded karyotype of tetraploid *Bromus ciliatus* L. *Euphytica* 146:177–182.
- TUNA, M., K.P. VOGEL, and K. ARUMUGANATHAN. 2006. Cytogenetic and nuclear DNA content characterization of diploid *Bromus erectus* and *Bromus variegates*. *Crop Sci.* 46:637–641.
- WAGNON, H.K. 1952. A revision of the genus *Bromus*, section *Bromopsis*, of North America. *Brittonia* 7:415–480.